

May 4, 1886.

Prof. W. H. Flower, LL.D., F.R.S., President, in the Chair.

The Secretary read the following report on the additions to the Society's Menagerie during April 1886:—

The total number of registered additions to the Society's Menagerie during the month of April was 170, of which 83 were by presentation, 23 by purchase, 11 by birth, 11 were received in exchange, and 42 on deposit. The total number of departures during the same period, by death and removals, was 119.

Amongst these special attention was called to:—

1. A fine example of a Lizard belonging to a new species of the genus *Ctenosaura*, which Mr. Boulenger described at the last meeting of the Society as *Ctenosaura erythromelas* (see above, p. 241), obtained by purchase April 3rd.

The exact locality of the specimen, which was purchased of a dealer at Liverpool, could not unfortunately be ascertained; but it is believed to be from some part of Central America.

2. A fine male example of the Lesser Koodoo, *Strepsiceros imberbis*, received in exchange from M. Cornély, of Tours, on April 7th.

Having lost the female, M. Cornély was good enough to part with the male of this rare Antelope in our favour. The specimen in question was originally obtained by one of Mr. Hagenbeck's collectors in Somali-land (see P. Z. S. 1884, pp. 45, 539).

3. A young male two-horned Rhinoceros, received in exchange from the Zoological Gardens, Calcutta, April 27th, and apparently referable to *R. lasiotis*, if this species is really distinct from *R. sumatrensis*. Dr. John Anderson, F.Z.S., has kindly favoured me with the subjoined note upon this interesting acquisition:—

"The young male Rhinoceros, lately received from the Calcutta Zoological Gardens, was brought into Rangoon on the 27th of March, 1884, while I happened to be there on my way to Japan. The animal had been captured a day or two before in the Bassein district, close to the sea, and, when first seen by its captors, it was in the company of its mother. The mother, however, escaped, I was told, by plunging into the sea and swimming away, leaving her young one behind. I at once secured it for the Calcutta Zoological Gardens. When I saw it in Rangoon it was only about 2 feet high at the shoulder, and was evidently quite a baby. Its skin was smooth and pinkish, and thickly covered with pale yellowish-grey hairs, somewhat curly, and as soft as wool, except on the front of the legs, where it was blackish-brown and much coarser than elsewhere. The positions of the two horns were well-defined, although these structures were only feebly developed. From its general appearance I concluded at the time that it was *R. lasiotis*."

Mr. E. L. Layard, F.Z.S., exhibited a rare Beetle of the family Cerambycidae (*Macrotoma heros*), obtained in one of the islands of the Fiji group.

This species was originally described and figured by Graeffe (Reis. Ins. Viti, 1868, p. 47, Taf. i.; see also the Stettin. entom. Zeitung, 1868, Taf. ii.). It was said to live in hollow trees. The specimen was intended for the National Museum.

Mr. Layard also exhibited a series of specimens of the genus *Bulimus* from New Caledonia and the adjacent islands, and some other interesting shells.

The following letter, addressed to the Secretary by Mr. F. W. Styan, F.Z.S., relating to some Chinese animals, was read:—

"Shanghai,
"12th March, 1886.

"I have lately procured from Ningpo the skin of a Hairy-fronted Muntjac, *Cervulus crinifrons*, the species described by you before the Society on the 20th January last. My specimen is a female, and as I believe the male in the Gardens of the Society is the only individual of the species that has yet been met with, a description of the skin may be interesting.

"The following are the measurements of the dry skin:—

	inches.
"From nose to root of tail	46 (appa- rently stretched)
Tail to end of bone	$6\frac{1}{2}$
Tail to tip of hair	$8\frac{1}{4}$
Heel to base of hoof	11
Shoulder to base of hoof	15
Nose to forehead between base of ears	9
Ears	4

"Upper parts rich dark glossy brown, mixed with black, darkest along the middle of the back. Belly and inner sides of thighs pure white, the line of demarcation very distinct except in the lower part of the thighs, where it merges gradually into dark brown. Tail above black, below pure white; a pale patch under the forearm; rest of the underparts dark brown. The brown of the neck gradually pales into reddish brown on the sides of the head; the nose-ridge dark brown; the longitudinal slits form a black V, the colour between them is a bright reddish brown, which turns into a fiery orange-brown in the tuft of bristly hair, rather more than two inches long, which rises from the tip of the forehead. On each side of this is a very small bony pedicle surmounted by short tufts of hair of the same colour. Ears at the base of the same hue, but not quite so bright, and fading into brown on the upper parts.

"In general appearance it much resembles both *Elaphodus michianus* and *Cervulus lacrymans*, having the dark-coloured body, tufted

forehead, and slender build of the former, and the yellow head and black slits along the face of the latter. It is, however, much larger than either, and apparently longer in the legs, compared with the size of body. Its fur is of a similar hard texture to that of *Elaphodus michianus*, but the colour is much richer and more glossy. The skull is attached to the skin, but I have not taken it out to examine. This species appears to be very rare; ever since the description of it first appeared, the man I employed to hunt has been specially looking for it, but has only procured this single specimen. When I first gave him a description of it he was quite incredulous, and said no such animal was known, nor would he believe in it until he actually came across this one.

“Last summer he procured for me two young of the *Elaphodus*, which I am not aware have been described before. They are apparently not more than two or three weeks old, but are almost exact miniatures of the adult, similar in colour, with a very pronounced frontal tuft, but no pale eyebrow, ears marked with white as in adult. On each side of the back is a row of not very distinctly marked white spots, and outside that again just the faintest suspicion of another row.

“I have also to record an interesting addition to the avifauna of China in the shape of *Hirundo savignyi*. Two birds, which I believe to be of this species, were killed at Peking last October, one of which is now in the Shanghai Museum. David records having seen Swallows with reddish-yellow underparts in Upper Mongolia, which doubtless were of the same species, but no record of its occurrence in China exists. Both are males, one an immature bird, and measure respectively $7\frac{1}{2}$ and 7 inches—the tail in the former being 4 inches, in the latter $3\frac{1}{2}$, not fully developed. In the adult the forehead and throat are deep chestnut, the lower parts uniform rich chestnut-buff; the nuchal collar is broad and complete, but a little mixed with chestnut. In the younger bird the colour of the forehead and throat is similar to that of the lower parts in the adult, while its lower parts are again paler, a bright buff, and the nuchal collar is broken in the centre.

“Whether *H. savignyi* is now admitted as a distinct species or is regarded as only a variety of *H. rustica* I do not know; but if the latter, its range is remarkably wide, and it is strange to find it where the parent form is unknown and replaced by a distinct species, *H. gutturalis*.

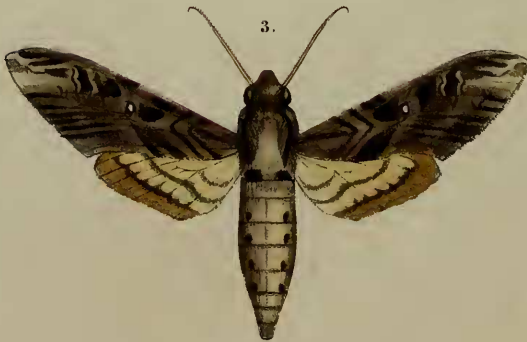
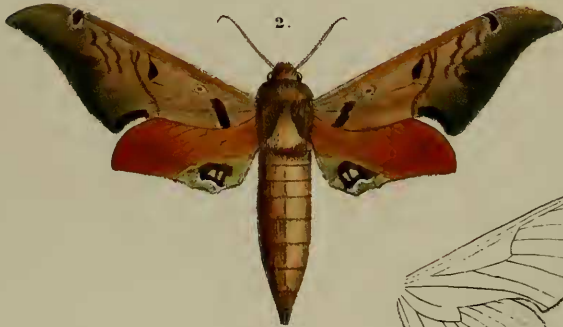
“I am, Sir,

“Yours faithfully,

“F. W. STYAN, F.Z.S.

“P.S.—A friend tells me that when in Peking in 1883 he saw Swallows with uniform brick-red underparts, but did not obtain specimens. It is probable the species is not uncommon there.”

The following papers were read:—



1. Remarks on four rare Species of Moths of the Family *Sphingidæ*. By W. F. KIRBY, Assistant in Zoological Department, British Museum (S. Kensington).

[Received April 16, 1886.]

(Plate XXVII.)

I am indebted to Prof. V. Ball and Mr. Nichols, of the Dublin Museum of Science and Art, in which most of the species noticed in this paper are contained, for an opportunity of carefully examining and figuring some of the more interesting *Sphingidæ* in the collection under their charge.

1. *CHÆROCAMPA MACULATOR*, Boisd. Lép. Hét. i. p. 274 (1874).

C. mœschleri, Ersch. Trudy Russk. Ent. x. p. 64, t. i. f. 1 (1876).

The identity of these supposed species has been suggested from the first. There is a specimen in the Dublin Museum which agrees with Erschoff's figure, except that it is not quite so dark, and the pale band of the hind wings is rather broader and has a slight pinkish tinge. This specimen was, I believe, received from Herr Möschler, labelled "*C. maculator*, Boisd., Colombia." Boisduval's type was from "Venezuela," and Erschoff's from "Colombia," the latter having been also received from Möschler. Boisduval's description agrees well with the Dublin specimen, except that he calls the pale band of the hind wings "*jaune terreux*," and seems to imply that the dark blotch on the fore wings is nearer the centre than is actually the case. But I am not disposed to attach too much importance to these trifling discrepancies.

2. *AMBULYX EOS*, Burm. (Plate XXVII. fig. 1.)

Philampelus eos, Burm. Desc. Rep. Arg. v. p. 350 (1878), Atlas, pl. 10. fig. 1 (1880).

The British Museum possesses a male from Buenos Ayres, presented by Walter de Rothschild, Esq., which differs so much from Burmeister's figure of the female that I have thought it worth while to figure it. The vertex, thorax, and fore wings are of a dull green, slightly inclining to olive above; the face and under surface of the thorax are greenish yellow, the base of the labrum and the knees being narrowly white. The antennæ are white behind, and reddish in front. The sides of the thorax above are of a much darker green than the centre, and are marked behind with a small white triangular spot; the first segment of the abdomen is also of a dark green, somewhat yellowish, the remainder being of a yellowish grey. The

fore wings are whitish at the base, this colour being narrowest at the costa; and rather below the costa is a small dark green spot near the base. On the inner margin, a dark green oblong mark curves upwards from the base, ceasing at one third of the distance from the costa, and rather beyond it is an oblong white spot with a dark-green centre. Below this, and beyond the oblong mark, the wing is obscurely marked with blackish, and from the upper curve of the oblong a dark obsolete mark curves towards the anal angle, before which it becomes more distinct, and is bounded outside by some whitish markings in the form of a W. In the middle of the wing are three obsolete transverse lines, ceasing at the subcostal nervure—the basal one dull green, the second obscurely blackish, and having an oblong black spot within its upper portion, and the outer one much waved, marked rather broadly with blackish above; beyond it, just below the subcostal nervure, is another blackish mark, like a broad V. The hind wings are reddish tawny, the hind margin being olive-yellow, most broadly so at the anal angle, above which it is surmounted by an irregular blackish blotch enclosing two white dots. Wings beneath yellowish green or greenish yellow, the fore wings being pale orange-yellow at the base to beyond the cell, and brighter orange along the costa; at the extremity of the cell is a blackish spot. The outer portions of the fore wings are marked with three obsolete green lines, converging towards a blackish spot at the anal angle, and the hind wings with three similar lines, which do not quite meet; the outer ones terminate in blackish blotches, between which stand two white dots.

The obscure shades and markings of the fore wings of this and the next species render them difficult to describe satisfactorily.

The fore wings are strongly falcate, and the anal angle is very strongly marked. The hind margin of the hind wings is bidentate beyond the anal angle.

3. *AMBULYX TITHONUS*, sp. n. (Plate XXVII. fig. 2.)

Very similar to *A. eos*, but the upper surface is of a much duller olive-brown; markings of the head and thorax nearly similar. Fore wings hardly white at the base and with a yellowish-olive band, slightly edged with white, running less obliquely from the inner margin just beyond the base to the median nervure, at which point it is broader than in *A. eos*; its outline is also more sinuous. Above the median nervure, and beyond it, is an obscure olive-green spot, flecked with white; at the end of the cell is a black spot, beyond which is a sinuous black line (double above) curving down to the inner margin; beyond it are two more waved blackish lines (the first double) running from the subcostal nervure half across the wing; the hind margin and anal angle are shaded into olive. Hind wings orange-tawny, paler at the anal angle, above which is a black blotch marked with two white dots, from which runs an ill-defined submarginal blackish stripe; the hind margin is also narrowly blackish. Wings beneath of a more uniform yellowish green than

in *A. eos* and the fore wings paler yellow at the base; the black discoidal spot is less strongly marked, and is followed by three short dusky lines on the costa; the hind margin is grey in the middle, bordered by a suffused blackish line running from the tip to the anal angle; on the inner margin, within the anal angle, is a short curved blackish line; nearer the base the inner margin is reddish. Hind wings beneath with a black spot at the end of the cell, and three obsolete greenish lines beyond (the middle most obscure), terminating in a black blotch, on which stands a yellowish-white spot, the two seen above having become united beneath.

The wings are rather less falcate than in *A. eos*, and the hind wings have only one tooth within the anal angle.

The example of this species was received by the Dublin Museum as "*Ambulyx lycidas*, Brazil;" but M. C. Oberthür of Rennes, who has kindly compared the figure with the type of that species (described by Boisduval, Lép. Hét. i. p. 191) from Brazil, informs me that the outline of the wings (which I have reproduced here from his sketch, Plate XXVII. fig. A) is very different.

4. PROTOPARCE ABADONNA. (Plate XXVII. fig. 3.)

Sphinx abadonna, Fabr. Ent. Syst. Suppl. p. 435 (1798).

Protoparce abadonna, Kirby, Trans. Ent. Soc. Lond. 1877, p. 238.

Sphinx godarti, MacL. King's Survey of Coasts of Australia, ii. p. 463 (1827).

I am glad to have an opportunity of figuring this species, from a specimen from Queensland in the Dublin Museum; it is singular that it has not yet been obtained for the British Museum. It is quite distinct from the common Australian *P. distans*, Butl. Macleay's description is so good as to render it unnecessary to redescribe the species here. I believe it to be *P. abadonna*, described by Fabricius from the East Indies, and I therefore retain his name provisionally, though I do not feel quite so certain of the correctness of this identification.

EXPLANATION OF PLATE XXVII.

Fig. 1. *Ambulyx eos*, ♂, p. 269.

2. — *tithonus*, sp. n., p. 270.

3. *Protoparce abadonna*, p. 271.

A. Outline of wing of *Ambulyx lycidas*, p. 271.

2. Observations on the Ovarian Ovum of *Lepidosiren* (*Protopterus*). By FRANK E. BEDDARD, M.A., F.R.S.E.,
Prosector to the Society.

[Received May 3, 1886.]

(Plates XXVIII. & XXIX.)

- I. Introduction, p. 272.
- II. Egg-membranes, p. 273.
- III. Germinal Vesicle, p. 276.
- IV. Follicular Epithelium and Development of Yolk, p. 279.
- V. Postembryonic Origin of Ova, p. 288.
- VI. Résumé, p. 291.

I. *Introduction.*

A recent memoir on the anatomy of the Dipnoi by Howard Ayers¹ contains some account of the ovaries and the ova in *Lepidosiren*², illustrated by several figures. The description of these organs is, however, mainly anatomical; and though in the figures some histological details of the ovary and the contained ova are to be found, their structure is not described. The author contents himself with remarking upon the similarity to the Amphibia, and all that I can find in his paper about the minute structure of the ovaries and ova is the following paragraph³:—"Die Structur der Eierstöcke ist direkt vergleichbar mit der der Urodelen. Die verschiedenen Stadien in der Entwicklung der Eier aus dem Keimepithel sind, soweit bei dem in Alcohol konservirten Material festgestellt werden konnte, wesentlich dieselben, wie sie für niedere Wirbelthiere constatirt sind. Wenn die Eier völlig entwickelt sind, so ist eine Hälfte ihrer Oberfläche pigmentirt (diejenige, welche gegen die freie Hälfte des Eierstockes gerichtet ist), während die andere Hälfte farblos bleibt"⁴. Furthermore, in describing the anatomical relations of the different parts of the genital system, Dr. Ayers takes occasion to remark that the sexual cells (both ovaries and testes) are inclosed in two delicate sacs—an outer peritoneal, and an inner formed by the connective-tissue stroma.

I shall refer more particularly to the appearances depicted in Ayers's figures in considering the structure of the ovaries and ova as I interpret them from my own preparations.

¹ "Beiträge zur Anatomie und Physiologie der Dipnoër," *Jenaische Zeitschr.* vol. xviii. (1885), pp. 479-527, 3 plates.

² The specimen studied by myself is from the Nile, and would therefore, according to some authors, be more properly termed *Protopterus*. Dr. Ayers shows reasons for assuming that there is really no generic distinction between the American *Lepidosiren* and the African *Protopterus*; the former name should therefore, on grounds of priority, be retained.

³ *Loc. cit.* p. 508.

⁴ This is a curious point of similarity to the ova of the Frog (see Balfour, *Comp. Embr.* vol. ii. p. 99; Pflüger, *Arch. f. d. ges. Physiol.* Bd. xxxi. 1883), not remarked upon by Ayers in his paper.





Concerning the origin of the ova I have no observations to offer. I shall therefore at once proceed to the discussion of the different parts of the ovum and its follicular epithelium.

II. *Egg-membranes.*

The question of the origin of the different egg-membranes and their homologies throughout the Vertebrate series has always been one of interest ; but the opinions held with regard to these points differ very much. Balfour considers it tolerably certain¹ that in most Vertebrata there are two egg-membranes present—(1) an outer structureless *vitelline membrane*, and (2) an inner perpendicularly striate *zona radiata*, both of which are formed as a differentiation of the egg-protoplasm. Of these two membranes the vitelline is obviously the first to appear ; the zona radiata subsequently makes its appearance, but is reabsorbed into the ovum some time before the latter is mature ; the vitelline membrane persists for a longer period, but eventually disappears. In the youngest ova of *Protopterus* I could detect no trace of any membrane ; as development proceeds a very delicate homogeneous membrane encircles the ovum. This membrane probably corresponds to the vitelline membrane, but I have no exact observations to offer on its origin ; judging from analogy it is a product of the egg-protoplasm, which at this stage (Plate XXIX. fig. 8) is of uniform granular appearance. At the same time the membrane was not at all firmly adherent to the ovum, but seemed to have a much more intimate relation to the follicular epithelium ; in sections that were less perfect than others this membrane was detached from the surface of the ovum.

In more mature ova—of the stage represented in Plate XXVIII. fig. 1—there was present, in addition to the vitelline membrane, a thick membrane lying beneath it, and evidently formed as a specialization of the peripheral layer of the ovum. For the most part this membrane was as distinct from the subjacent protoplasm of the ovum as is shown in Plate XXIX. fig. 2. Here and there it appeared to pass gradually and without any break into the substance of the protoplasm. This membrane shows radial striations (Plate XXIX. fig. 2), and appears to me in all probability to correspond to the zona radiata of other Vertebrata. The extreme thinness of the vitelline membrane as compared with the zona radiata is illustrated in Plate XXIX. fig. 2. In this stage there was no trace of any formation of yolk except that the egg-protoplasm has taken on a reticulate arrangement (see Plate XXIX. fig. 2) in preparation for the yolk-formation soon to commence.

In the next stage, in which yolk-formation has already commenced, the conditions of the egg-membranes are slightly different, the difference principally relating to the outer vitelline membrane. The vitelline membrane in this stage is very markedly thicker than in the previous stage ; it is also much more intimately connected with the follicular epithelium than with the zona radiata. The latter

¹ Comp. Embr. vol. i, p. 50.

membrane shows signs of its subsequent reabsorption into the ovum, the lower margin being rather less distinct than in the earlier stage. At no time is the zona radiata so distinctly "membranous" as the vitelline membrane; it always has a granular appearance, and if it were not for the fine vertical striæ, which are presumably the expression of pores, would be regarded as merely a superficial layer of the protoplasm appearing more deeply stained because of its firmer texture. If the vertical striation be really due to protoplasmic processes traversing the zona radiata, this latter must be regarded as a distinct metamorphosis of the superficial layer of the ovum; otherwise, if it really has retained its protoplasmic character, there would be no necessity for special protoplasmic filaments to pass through its substance: the whole layer would serve equally well as a conductor of nutritive material. The disappearance of this membrane, which commences with the commencing formation of yolk, is complete in the later stages of the maturation of the ovum; and the disappearance is easier to understand on the assumption that the zona radiata is only but little changed from its original protoplasmic condition, its reabsorption being therefore a kind of solution. On the other hand, the thinning of the vitelline membrane in the later stages of egg-development is possibly purely mechanical, being due to the extension of an elastic membrane through the increasing bulk of the egg-contents.

The pores in the zona radiata are very generally believed to admit processes of the follicular epithelium, and where no imperforate membrane exists between the zona radiata and the follicular epithelium, as in Mammals, it has been actually demonstrated that such is the case.

In Elasmobranchs Balfour¹ has described an enlargement of some of the follicular cells as the ovum approaches maturity; these are doubtless concerned with the nutrition of the ovum, but they cannot (?) come into actual contact with it because the vitelline membrane divides them. It is a significant fact, however, that at this period the vitelline membrane becomes extremely thin, so that it would evidently favour osmosis. In this case the perforations of the zona radiata may still be the expression of pores which contain prolongations, not of the follicular cells, but of the egg-protoplasm, which thus takes an active part in its own nutrition, as in the lower forms, and is not merely passively fed by the follicular epithelium.

This may well be the case with *Lepidosiren*, though I have been unable actually to demonstrate the protoplasmic contents of the pores in the zona.

During this second stage of the egg-development, while the yolk is in process of formation, and there is therefore a special need of extra nutrition, not merely are these pores in the zona radiata, but in the more highly refracting membrane outside of this (Plate XXIX. fig. 5), which I believe to be the thickened vitelline membrane of earlier stages.

These pores are very obvious indeed, and impossible to be over-

¹ Quart. Journ. Micr. Sci. 1878, p. 405.

looked in good sections. The vitelline membrane in earlier stages is so thin that I have found it impossible to detect any pores; it may be that they are present, or that the nutrition of the ovum in the earlier stages is carried on, as suggested above, by osmosis, while during the later stages, when the formation of yolk is going on and the need for nutrition increased, direct contact between the follicular cells and the ovum is necessary to convey adequate nourishment.

In the stage represented in Plate XXVIII. fig. 3, which is characterized by the extraordinary proliferation of the follicular cells and their migration into the interior of the ovum, there was no trace whatever of any membrane. The ovum lies within the follicular epithelium, and in actual contact with its cells. Indeed the very migration of the follicular cells into the ovum would necessitate the absence of such a membrane, and there were, at any rate, no traces of it except in the well-marked limiting membranes (see Plate XXIX. fig. 7) of the follicular cells, which, however, I never observed to be separated from the cells themselves, and were continuous all round them. The absence of any such membrane round the ova of this stage is one of the strongest arguments against regarding them as a stage intercalated between the last and the next to be described. Into this question I shall enter later.

In the latest stages, in which the ovum is entirely occupied by yolk, the follicular epithelium is separated from the contents of the ova by an extremely fine and delicate homogeneous membrane (Plate XXIX. fig. 6); this membrane probably corresponds, in some ova at least, to the vitelline membrane which has persisted after the disappearance of the internal zona radiata. In some ova belonging to this stage, the occurrence of a few scattered cells through the substance of the yolk appears to indicate that they have been derived from ova belonging to the stage just referred to; in these also a thin delicate membrane lay between the ovum and the surrounding follicular epithelium. In this case the membrane must be regarded as a new formation, though perhaps still homologous with the vitelline membrane.

In the number and structure of its membranes the ovum of *Lepidosiren* appears to be related much more nearly to the Elasmobranchs than to the Amphibia, with which group the general anatomical structure of the reproductive organs more closely corresponds. In the Amphibia in fact, according to Waldeyer and Kollessnikow, there is only a single delicate membrane, developed comparatively late, and showing a radial striation. Götte's observations on *Bombinator*¹ point to the existence of a single membrane, clear and structureless, which arises by a metamorphosis of the external layer of the ovum. In *Triton* Iwakawa² describes and figures a single structureless membrane surrounding the ovum. In these cases the single membrane evidently represents the membrane in *Lepidosiren* which I have termed vitelline. The discrepancies in the observations of these authors on the structure of the membrane,

¹ *Entwicklungsgeschichte der Unke*, p. 19.

² *Quart. Journ. Micr. Sci.* vol. xxii. (1882), p. 274, pl. xxiv. figs. 2, 4-26.

whether it is really structureless or radiately striate, are possibly to be explained by supposing that, as in *Lepidosiren*, it is structureless at one time and striate at another.

So also with the observations of Brock upon the Teleostean ovum. This anatomist figures (*loc. cit.* pl. xxviii. fig. 7 f, pl. xxix. fig. 6 B e) two ova, both of which are provided with two egg-membranes: in the one the outer egg-membrane is striate, while in the other it is unstriate; in the latter case it is considerably thinner than in the former, and the processes of the follicular cells, whether by accident or design, are drawn as if stopping short at the outside of the membrane. Brock's figures seem to me to point to the conclusion that the outer egg-membrane (vitelline membrane) arises, as in *Lepidosiren*, as a differentiation of the outer layer of the egg-protoplasm, and is subsequently perforated by processes of the follicular cells as the ovum approaches maturity. On the other hand, the perforations in the zona radiata would seem in this case to be caused, as suggested above, by protoplasmic strands radiating outwards from the ovum. The observations of Owsiannikow appear to contradict this explanation. Owsiannikow has figured (*loc. cit.* pl. i. fig. 3) the branching of the processes of the follicular cells after they have passed through the outer membrane, in which the pores are wider apart, to fit into the more closely arranged pores of the inner membrane.

III. History of the Germinal Vesicle.

My observations on the development of the germinal vesicle are unfortunately rather meagre. I have been unable to trace it continuously from the youngest to the most mature ova. The principal lacuna in the history of the germinal vesicle is the very interesting stage characterized by the immigration of the follicular cells into the substance of the ovum. In this stage I could observe no appearance whatever of a germinal vesicle, which is much to be regretted, as it would be interesting to know what are its relations to the immigrating follicular cells¹.

I observed two distinct stages in the development of the germinal vesicle which will now be described. The first stage is found in young ova, in which the yolk-formation has not yet begun. The germinal vesicle is of an oval form, and lies excentrically within the ovum; it is bounded externally by a very fine membrane in *Ceratodus*, according to Ayers's figure (*loc. cit.* pl. xviii. fig. 76). In my own preparations (Plate XXIX. figs. 3, 4) the limiting

¹ Dr. Balbiani has described in the egg of *Geophilus* (Zool. Anzeig. Nos. 155, 156) a formation of cells from the germinal vesicle which pass through the substance of the ovum, and ultimately range themselves round its periphery to form a follicular epithelium. These stages are depicted in a series of woodcuts, some of which bear not a little resemblance to the stage in the maturation of the ovum of *Lepidosiren* described above. It is possible that the appearances described by Balbiani may ultimately be reconciled with those described by myself in the present paper. Balbiani's observations have not, however, been confirmed by the recent researches of Heathcote (Quart. Journ. Micr. Sci. 1886), though in many insects' ova other observers have noted similar processes.

membrane of the germinal vesicle is not always very obvious; but as there is a sharp contrast between the protoplasm of the germinal vesicle and the surrounding substance of the ovum (indicated by the much deeper staining of the former by borax carmine), there comes to be an appearance of a delicate membrane surrounding the germinal vesicle; this membrane has not a double contour.

In younger ova there is a very distinct membrane bounding the germinal vesicle externally; this membrane is more easily to be distinguished in my preparations from the fact that it is very deeply stained.

Although the boundaries of the germinal vesicle are distinct enough, there is no cavity dividing it from the egg-protoplasm; the granules of the latter are everywhere in contact with the germinal vesicle. In several preparations the germinal vesicle had shrunk; but in every case observed by me the wall of the germinal vesicle was covered with egg-protoplasm granules, thus showing that the spaces surrounding the germinal vesicle in that figure are not natural, but due to alterations caused by the contraction of the germinal vesicle.

The interior of the germinal vesicle is occupied by a finely-granular matter, which is almost homogeneous throughout. In certain tracts, however, the granules are more deeply stained and often larger; these granules form a reticulum (Plate XXIX. fig. 3). In the ovum of *Triton*, Iwakawa illustrates (*loc. cit.* pl. xxiv. fig. 27) a very similar condition of the nucleoplasm. The germinal spots are very numerous, and form a layer surrounding the germinal vesicle; the latter is shown on a superficial view in fig. 3, and in transverse section in Plate XXIX. fig. 4. The germinal spots are of very varying size, and usually oval or circular in form; borax carmine stains them more deeply than the surrounding nucleoplasm; they are evidently not homogeneous, but appear to consist of an outer sheath of stout consistency, and very deeply stained by the reagent, and within this an apparently more fluid core which is not deeply stained.

The presence of numerous germinal spots is figured by Ayers for both *Ceratodus* (plate xviii. fig. 76) and *Lepidosiren* (plate xvii. fig. 27).

It is also characteristic of the Teleostean ovum¹, and is mentioned by Messrs. Balfour and Parker² in *Lepidosteus*. Among Amphibia *Triton* shows the same condition of the germinal spots. In ova of the stage represented in Plate XXVIII. fig. 2, the substance of the ovum which immediately surrounds the germinal vesicle differs from the rest in being more loosely compacted.

In ova which are distinguished by the enormously increased functional activity of the follicular epithelium, the germinal vesicle could not be found. In all probability, however, my failure to find the germinal vesicle is not due to its absence.

¹ Brock, "Beiträge z. Anatomie und Histologie der Geschlechtsorgane der Knochenfische," Morphol. Jahrb. Bd. iv. (1878) p. 505, pl. xxviii. figs. 8, 11.

² "On the Anatomy and Development of *Lepidosteus*," Phil. Trans. 1884.

In older ova the germinal vesicle has altered somewhat from the characters which it presents in the earlier stages of the maturation of the ovum. In Plate XXIX. fig. 1, I have sketched a germinal vesicle precisely as it appeared in transverse section. It will be noticed, in the first place, that the germinal vesicle is very sharply marked off from the surrounding substance of the ovum, and in the section figured has become separated from it throughout a considerable area; this separation is no doubt due to shrinkage, but serves to show the very trenchant line of division which separates germinal vesicle and ovum, since no yolk-spherules were found to remain adherent to the germinal vesicle.

The substance of the germinal vesicle in ova of this stage of development has become specialized into an outer peripheral portion and a central core. These two areas of the germinal vesicle are almost as sharply marked off from each other as is the outer layer of the germinal vesicle from the surrounding egg-protoplasm and yolk. This is clearly shown in the same figure (Plate XXIX. fig. 1), and, as in the first case, is probably due to shrinking of the germinal vesicle when plunged into the preservative reagent. Along the upper side of the preparation illustrated in the figure already referred to, the central core of the germinal vesicle has shrunk away from the external sheath; along the lower margin of the germinal vesicle the contraction has not caused a separation of the two constituents, but a split in the outer layer, which I have not indicated in the figure.

The outer coat of the germinal vesicle is very easily distinguishable from the inner core; it is much more finely granular in structure, appearing occasionally almost homogeneous, and has become stained a pale pink. The inner core is more coarsely granular, and has a yellowish tinge, hardly owing to the non-penetration of the staining reagent, since the imbedded nucleoli were deeply stained.

The substance of the internal core contained elliptical spaces here and there, which are possibly themselves due to contraction. The boundary line between the central core and the peripheral layer is also marked by the nucleoli, which are for the most part situated in a single layer at the extreme periphery of the central core. A few, however, as indicated in the figure, are to be found in the more central regions of the core. The nucleoli were extremely conspicuous owing to their vivid staining with the reagent, and appeared to be solid, being uniformly stained throughout. In the earlier stages of the germinal vesicle mention has already been made of the annular appearance of the germinal spots. The germinal spots were very unevenly distributed and of varying size, but were never found in the peripheral layer of the germinal vesicle.

In *Triton*, Iwakawa has described what appear to be very similar changes in the germinal vesicle, though there is some little difference in detail; as the egg approaches maturity the germinal spots move in towards the centre of the germinal vesicle, leaving a homogeneous, more deeply stained peripheral area.

IV. *The Follicular Epithelium and the Formation of Yolk.*

In the youngest ova (Plate XXIX. fig. 8) the protoplasm is dense and solid, staining deeply with borax carmine; the uniform appearance of the egg-contents indicates that no formation of yolk has at present commenced.

In the next stage, where the zona radiata is well developed (Plate XXVIII. fig. 1), the protoplasm of the ovum is less dense and has acquired here and there a reticulate arrangement, which is well shown in the figure referred to.

In ova slightly more mature (Plate XVIII. fig. 2) the formation of the yolk is in active progress, though for the present confined to limited areas of the egg-protoplasm. None of my sections display any ova which show the first beginning of yolk-formation. In Plate XXVIII. fig. 2, it will be noted that the yolk appears in patches usually spherical in shape and larger or smaller; the yolk has the form of minute spherules and aggregations of spherules, which are easily distinguishable from the surrounding protoplasm, which is also granular, by their more coarsely granular appearance. They have also been stained much more darkly by the borax carmine.

The yolk-spherules invariably make their appearance in the interspaces between the reticulations of the egg-protoplasm. There is thus no doubt that the yolk is actually formed in the interior of the ovum at the expense of the egg-protoplasm; the reticulation of the egg-protoplasm, invisible in earlier stages, but completed before the appearance of yolk, is probably a preparation for the formation of the latter, which is received when formed into the interspaces between the protoplasmic strands.

Ova of the next stage (Plate XXVIII. fig. 4) show the yolk-spherules well developed and filling up the entire ovum; the spherules themselves are small and of varying size; occasionally numbers of yolk-spherules had run together to form irregular shaped masses; these yolk-masses, owing to their size and impenetrability, were invariably left unstained.

The yolk at this period entirely fills the ovum, and is spread throughout it in a perfectly uniform fashion; there was no indication of any peripheral layer free, or nearly free, from yolk.

The ovum displayed in Plate XXVIII. fig. 4 is remarkable for the fact that the yolk is distinctly differentiated into two layers—a thin peripheral layer, and a central mass; the boundary between the two was perfectly distinct, there being an absolute break, a narrow line perfectly free from yolk-spherules; the outer layer was also rendered more conspicuous by the lighter staining of the reagent. I have noticed several ova among my sections which displayed this curious differentiation.

Throughout its whole development the ovum is surrounded by a single layer of follicular epithelium-cells; these cells are flattened as in the Amphibia, and have a large deeply staining nucleus. In most cases a *membrana propria folliculi* could be detected outside these cells.

It seems to me to be fairly certain that the ova represented in Plate XXVIII. figs. 1, 2, 4, are progressive stages in egg-development: there is a gradual increase of size accompanied by various changes in the egg-contents, the germinal vesicle, and the egg-membranes, which all tend to prove the truth of this supposition. All these different stages were frequently to be observed in a single section. In the same sections were a number of very peculiar ova, displayed in Plate XXVIII. fig. 3; these were for the most part intermediate in size between ova of the third stage (fig. 2) and the more mature ova (fig. 4); in a few cases, however, they were distinctly smaller than ova of the third stage. This last fact would be hardly sufficient of itself to prove that these ova do not form a stage intercalated between Stages 3 and 4, because there is often some irregularity in size; larger ova, particularly if they are not much larger, could not be positively regarded as more mature than smaller ova. In the first place, however, the structure of these ova and the conditions of the follicular epithelium are so markedly different from ova of any other stage, that it seems difficult to assign them to the same series; and, in the second place, I have been able to observe no transitional stages between these ova and those belonging to Stages 2 or 3. On the other hand, these ova eventually acquire the same appearance as ova that have evidently passed through Stages 2 and 3; to this point I shall return later. I must for the present leave it an open question as to whether these ova form part of the same series as those displayed in Plate XXVIII. figs. 1, 2, 4, or whether the ovary of *Protopterus* contains ova of two kinds which follow a different course of development though they ultimately come to be identical in appearance.

These ova (Plate XXVIII. fig. 3) are surrounded by a follicular epithelium which, like that of the other ova, consists of a single layer of cells; these cells are long and somewhat columnar in form (Plate XXIX. fig. 7); they are limited by a distinct membrane and contain a darkly stained nucleus as well as a number of *highly refracting round particles which resemble in every respect the yolk-spherules of the contained ovum*. These follicular cells rest upon the surface of the ovum, and there is no trace whatever of any membrane separating them from the ovum.

The connective-tissue sheath of the follicle was very distinctly marked off from the surrounding ovarian stroma; near to the periphery of the ovum were an immense number of blood-capillaries of large size and gorged with blood. These capillaries, although probably belonging to the stroma-sheath, were in many cases pressed down among the epithelial cells of the follicle, appearing as if they were actually lying between the cells; this remarkable appearance of the blood-vessels is illustrated in Plate XXIX. fig. 7, which represents a portion of the periphery of such an ovum very highly magnified. The interior of the ovum contained abundant yolk; but in no case did I succeed in finding any trace of a germinal vesicle. The yolk consisted of highly refracting spherules which were for the most part of small size, but here and there were very much larger spherules.

The structure of these ova and the surrounding follicle is extremely remarkable, and quite unlike any other ova that I have seen in transverse sections of the ovary of *Protopterus*. But the peculiarities of these ova do not end here.

Scattered throughout the substance of the yolk are an immense number of cells more or less spherical in form (Plate XXVIII. fig. 3, c).

These cells were limited in most cases by a very distinct external membrane; *their contents are a mass of rounded bodies which are quite indistinguishable from the yolk-spherules of the ovum*, and strands of granular protoplasmic substance; furthermore there is a distinct and large nucleus deeply stained by borax carmine, and within this a number of nucleoli and granules.

These cells appeared to be in a condition of active multiplication, the various stages of which are indicated in Plate XXIX. figs. 9-20. In fig. 10 the nucleus is constricted in the middle; in fig. 11 the nucleus has divided; in fig. 12 the two cells have become distinct but lie close together; in fig. 18 cell-division has evidently gone on very rapidly, as there is a nest of four cells pressed closely together and occupying a common cavity in the yolk. In some cells the amount of yolk-granules present was considerably less than in others. Occasionally (figs. 19, 20) the yolk-particles had run together to form a single large droplet.

In a few cases I observed (fig. 15) the nucleus to be thrust altogether without the cells; and here and there within the substance of the ovum were apparently nuclei without any cells. I am not inclined, however, to lay too much stress upon the last mentioned fact, because it would be rather difficult in any case to detect the boundaries of one of these cells if it were packed quite full of yolk-spherules.

In other cases (fig. 13) the nucleus had become paler in colour (less acted upon by the staining reagent) as well as more homogeneous. Nuclei of this kind might easily be mistaken for larger yolk-spherules; indeed my only reasons for believing them to be altered nuclei are their similarity in size and shape to the more normal nuclei, their occurrence in cells that have become emptied of their contents, and the fact that they are rather more deeply stained than the surrounding yolk.

Concerning the nature of these bodies there appears to me to be three possibilities:—either (1) they are similar to the white yolk-spherules of the Fowl's egg; or (2) they are follicular cells which have migrated into the interior of the ovum; or (3) they are cells which have been formed anew within the substance of the ovum.

The first alternative, that the structures in question correspond to the white yolk-spheres of birds, seems at first sight to be a likely explanation of their occurrence, especially since they are only to be seen in comparatively young ova. The white yolk-spheres of birds¹ are rounded bodies containing one or more highly refractive nucleus-like bodies in their interior; but these apparent nuclei are really

¹ Foster and Balfour's 'Elements of Embryology,' p. 16.

very dissimilar to true nuclei, and the sphere has no limiting membrane. It is doubtful therefore whether they can be regarded as cells, though it is probable that, as the segmentation of the ovum advances, the white yolk is directly converted into cells. Now in the cell-like bodies which I have described in the immature ovum of *Lepidosiren* there is a very distinct and obvious nucleus (figs. 9-20), which is in fact entirely similar to a nucleus of one of the follicular cells; it is deeply stained by borax carmine and unevenly stained, so that it has the appearance of being formed of a meshwork of condensed protoplasm, the interspaces of which are filled by a homogeneous substance which is less acted upon by the reagent. In some instances there was more than a single nucleus to each of these cells, but it is quite impossible to confound these nuclei with the surrounding particles of yolk. Furthermore, in many cases the limiting membrane of the cells was distinctly visible (figs. 9 &c.); and the fact that the cell-contents were hardly acted upon by the staining fluid rendered the perception of this membrane easier. There seems to be but little doubt that these structures are veritable cells, and are not in any way comparable to the white yolk-spheres. The question then arises, What is the origin of these cells? Are they formed anew within the substance of the ovum, or have they migrated from the follicle into the interior of the ovum?

The former supposition is supported by no facts that I have been able to note, and it is distinctly negated by other facts.

In the first place, these cells are very closely similar to the cells of the follicular epithelium; like them they are bounded by a distinct limiting membrane; the contents of both consist of protoplasmic strands and numerous highly refractive particles similar to the yolk-particles; the nucleus is identical in shape and size; and the behaviour of both to the staining reagent is precisely the same. This series of facts would, however, be hardly regarded as proof that these cells have originated from the follicular epithelium; it might be supposed that the cells have arisen within the ovum, and that some of them have migrated to the periphery to form the follicle, as has been stated by various observers to be the case in certain other ova (see p. 276); but the immense vascular development round the follicular epithelium that has been already mentioned seems to indicate that the main activity is centered in these latter cells; and this fact, coupled with the additional fact that in certain instances there were masses of migrating cells evidently in course of being budded off (Plate XXVIII. figs. 5, 6) from the follicular epithelium, seems to indicate that the second supposition as to the origin of these cells is correct, viz. that they are formed by the proliferation of the follicular cells and migrate into the interior of the ovary.

The migration of these cells also explains the absence of a limiting membrane to the ovum. A "formed" membrane, however thin, would evidently prevent such a migration.

It appears to me possible to make another statement as a deduction from the facts just detailed: *that the follicular epithelium-cells secrete the yolk which is conveyed to the interior of the ovum by*

means of the proliferating follicular cells. I do not mean to assert that these ova do not also form yolk endogenously, as I have observed in other cases (Plate XXVIII. fig. 2); but the similarity between the contents of the follicular cells and their derivatives which migrate into the interior of the ovum, on the one hand, with the yolk-spherules of the ovum, on the other hand, coupled with the fact of the subsequent disintegration and disappearance of the immigrated cells, seems to me to necessitate the conclusion that at least part of the yolk is so formed.

Unfortunately I am quite unable to record any observations as to the earlier stages of these ova; they may be a stage intercalated between Stages 3 and 4, as already suggested. In favour of this supposition are the following facts:—(1) that for the most part these ova are intermediate in size between the presumed earlier and later stages; (2) that there is no proof of their independent origin; (3) the unlikelihood (?) of there being two kinds of ova with a different process of growth.

Against such a supposition I may adduce the following arguments:—(1) the absence of any transitional stages between these ova and the presumed younger stages; (2) the disappearance of the vitelline membrane during this stage and its subsequent reappearance, or at least the appearance of a similar membrane.

Whatever may be the origin of these ova, they come ultimately to resemble in every particular the ordinary mature ova. I have fortunately succeeded in obtaining sections of an ovum considerably larger than that just described, which presented the following characters:—The follicular epithelium was considerably reduced in importance, as was also the accompanying network of blood-capillaries. Between the follicular epithelium and the ovum was a distinct membrane excessively thin; there were hardly any traces left of the immigrating follicular cells present in such great numbers in the earlier stages; I noted perhaps one or two in as many sections.

It is interesting to observe that if these ova, characterized by the formation of the yolk from the follicular cells, are really different from the other ova, they are in certain respects more Amphibian like than the other ova; not in the immigration of follicular cells, but in the late appearance of a single thin membrane shutting off the ovum from the follicular epithelium with which it was previously in contact. Götte, in his 'Entwicklungsgeschichte der Unke,' makes the following statement (p. 16):—"Ferner kann man bei der Anwendung des Wassers nachweisen dass der Follikelinhalt noch unmittelbar die Zellen berührt, dass aber die Grenze zwischen beiden Theilen eine sehr scharfe ist und sie durchaus nicht continüirlich zusammenhängen." It is only later that a membrane surrounding the ovum and separating it from the follicular cells appears.

Similarly Iwakawa's observations upon *Triton*¹ show that in the young stages the follicular cells are in contact with the body of the ovum. In more mature ova a membrane comes to surround the

¹ Quart. Journ. Micr. Sci. vol. xxii. p. 270.

body of the ovum; this membrane does not appear until after the yolk has begun to be formed.

Leaving the question as to the origin of these ova undecided for the present, the penetration of the follicular epithelium into the interior of the ovum and the formation of yolk by the follicular cells are in my opinion strongly supported by the facts that I have been able to bring forward. I will now compare these facts with similar observations on other ova.

A migration of follicular cells into the ovum has been recorded by several writers, but other writers have thrown doubts upon the accuracy of these observations.

In Elasmobranchs and Amphibia nothing of the kind has been recorded; Balfour, in studying the ovarian ova of *Scyllium*, particularly directed his attention to this point, but was unable to find any trace whatsoever of cells such as have been described by His in the Teleostean ovum; he suggests indeed that His may have mistaken the white yolk-spherules for such cells; the resemblance of white yolk-spherules to cells is not a little striking, and may easily have led to mistakes.

With regard to the Teleosteans, however, there is some variety of opinion as to this point. His¹ has described a migration of the follicular cells through the pores of the zona radiata into the interior of the ovum; but Brock (*loc. cit.* p. 558) doubts the truth of this observation, not merely because he did not himself succeed in seeing any such migration, but because it appeared to him inexplicable that if there were so general an immigration the follicular epithelium should yet maintain its continuity.

The most recent writer on the subject whose memoir is known to me is Owsjanuikow². This author describes in detail a number of facts relative to the structure of the Teleostean ovum which are often somewhat difficult to understand. With regard to the supposed immigration of cells (leucocytes) into the interior of the ovum, believed by His to occur, this author states that it has not been observed by him, and that further the necessity for such a process of nutrition does not exist, since nutritive material is supplied to the ovum through the processes of the follicular cells, which are so universally admitted to pass through the egg-membrane. At the same time Owsjanuikow describes in *Osmerus* and *Acerina* a peculiar condition of the yolk, also referred to by His, but denied by others, which in a certain degree is similar to the condition which I have described in the present paper in *Lepidosiren*. The yolk-bodies ("Dotter-Kugeln") contained in many cases nuclei often difficult to show and needing most complicated processes for their demonstration; in these structures, which the author calls cells, the oil-drops take their origin. Without additional investigations it does not seem to me permissible to regard these bodies as true cells; their appearance in Owsjanuikow's figures (pl. ii. figs. 22, 23) is very

¹ 'Eierstock der Knochenfische,' p. 22, &c.

² "Studien über das Ei, hauptsächlich bei Knochenfischen," Mém. d. l'Acad. d. St. Pétersb. t. xxxiii. no. 4.

much like that of the white yolk-spheres of Sauropsida. In any case these bodies are not supposed to have an extrinsic origin, but to arise within the ovum. On the other hand, a penetration of follicular cells through the micropyle (*loc. cit.* pl. i. fig. 6) appears really to occur in many osseous fish and to be comparable to the proliferation into the ovum of the follicular cells in *Lepidosiren*.

Kolessnikow¹ confirms the accuracy of His's results as to the entrance of leucocytes into the ovum, but does not think this process to have much functional importance.

In Mammals a number of observations have been published which tend to show that there is a migration of cells, which is evidently comparable to the facts which I have detailed above in *Lepidosiren*. Lindgren² has described such a migration of follicular cells, and figures an ovum which is half filled with unaltered follicular cells. Von Sehlen³ and H. Virchow⁴ have confirmed the accuracy of Lindgren's observations. More recently Schäfer⁵ has described a remarkable series of changes in the Rabbit's ovum which do not altogether tend to the same conclusion. In young ova, which are as yet surrounded by a follicle consisting of only a single layer of cells, peculiar cells make their appearance in the peripheral regions, and ultimately form a single layer of cells which surround the ovum, lying beneath the follicular layer. Schäfer believes that these cells are not derived from the follicular layer, but they originate in the ovum. He compares very justly his own observations with those of Kuppfer on *Ascidia canina*. Kuppfer⁶ had shown that cells appear in the interior of the ovum and range themselves round its periphery. Kuppfer, however, believed that these cells originate in the ovum itself, and are not, as Kowalevsky supposed, a product of the follicular epithelium. His statements therefore are in complete accord with those of Schäfer; while Lindgren, von Sehlen, and H. Virchow describe a process in the maturation of the mammalian ovum which is more comparable to that described by Kowalevsky in the case of the Ascidians. The latest writer on the mammalian ovum, Mr. Heape, did not find any such migration of follicular cells, and concludes that the observations put on record by Lindgren, von Sehlen, and Virchow are based upon abnormal processes. It is to be noted, however, that the type studied by Heape⁷ (Mole) was not studied by any one of these naturalists, and this fact may possibly account for the discrepancies in their statements. In the latest edition of Quain's 'Anatomy' it is suggested that the entrance of follicular cells into the ovum described by Lindgren, von Sehlen, and H. Virchow may be an abnormal process and not a regular

¹ Archiv f. mikr. Anat. vol. xv. (1878) p. 399.

² Arch. f. Anat. u. Phys. 1877.

³ Arch. f. Anat. u. Phys. 1882.

⁴ Arch. f. mikr. Anat. Bd. xxiv. (1884).

⁵ Proc. Roy. Soc. vol. xxx. (1880) p. 243.

⁶ Arch. f. mikr. Anat. Bd. viii. See also the papers of many others (Sabatier, Roule, Fol) on the Ascidian ovum, and the facts referred to in footnote on p. 276, *suprà*. These have been lately summed up in Quart. Journ. Micr. Sci., June 1886, by Mr. Arthur Thomson.

⁷ Quart. Journ. Micr. Sci., Feb. 1886.

occurrence. I would suggest myself that this migration of follicular cells in the Mammalia is a record of what occurred in their Dipnoan ancestors¹, where the migration of follicular cells into the interior of the ovum was an important process in connection with the formation of yolk.

It is, however, among the Invertebrata that the most striking resemblances to the immigration of follicular cells in *Lepidosiren* are to be found, and more particularly in the Cephalopoda.

Some remarkable facts with respect to the nutrition of the ova of *Sepia* have been discovered by Lankester, which are analogous to the facts recorded by myself in *Lepidosiren*. In *Sepia*² the ova are surrounded by a single layer of follicular cells which are supplied externally with an abundant vascular network. The epithelial layer becomes folded in a complicated fashion, and the folds project into the interior of the ovum (*loc. cit.* pl. 12. fig. 23); the cells of the epithelium take on a character resembling that of the goblet-cells, and pour out their contents into the ovum; moreover the cells also proliferate and pass off into the interior of the ovary (*loc. cit.* pl. 12. fig. 25), becoming gradually absorbed.

Kowalevsky³ has described a proliferation of the follicular cells of Ascidians which migrate into the interior of the ovum, and eventually form (*loc. cit.* pl. 10. figs. 2-4) a complete layer round it, so that the follicle comes to be two layers deep; the outer layer, which is made up of very much larger cells, represents the original follicular epithelium, while the inner layer consists of very much smaller cells.

In many of the lower Invertebrata the ovum is largely nourished at the expense of the surrounding cells. In the Platyhelminthes a peculiar organ, the vitellarium, elaborates yolk-particles which are subsequently absorbed by the ovum; analogous processes take place in many Insects. In all these cases the ovum retains the capacity, inherited from its Protozoan ancestor, of feeding by the intussusception of solid particles.

All these facts seem to me to be directly comparable to what has been described above in *Lepidosiren*. The secretion of yolk by the follicular cells in the Platyhelminth and the absorption of this yolk by the ovum only differs in degree from the proliferation of the follicular cells in *Sepia* and *Lepidosiren* and their subsequent absorption by the ovum.

I may say a few words with regard to the special fact that the yolk is largely elaborated with follicular cells and conveyed to the ovum by the proliferation of these cells and their subsequent disintegration in the interior of the ovum. Such a formation of yolk in the Vertebrate ovum has not been put beyond a doubt; indeed most observations on the subject seem to show that the yolk is generally

¹ I imagine that few will dispute Prof. Huxley's opinion that the Mammalia in the course of their evolution have passed through a Dipnoid stage (see P. Z. S. 1880, p. 661).

² "On the Developmental History of Mollusca," Phil. Trans. 1875, p. 43.

³ "Weitere Studien über d. Entwicklung d. Ascidien," Archiv f. mikr. Anat. Bd. vii. (1871) p. 101.

formed in the interior of the ovum itself and has not an extrinsic origin.

Kolessnikow¹, however, concludes his paper on the Teleostean and Amphibian ovum with the statement that the yolk is chiefly a product of the follicular epithelium, which behaves in this respect like a gland. Apart from this fact, the follicular cells do, however, play an important part in supplying the ovum with nutriment in most Vertebrata; but this is not in the form of yolk, which is subsequently elaborated in the ovum itself. In Elasmobranchs Balfour has noted² that certain of the cells become larger than the others, and apparently communicate within the substance of the ovum into which they pour their contents. Heape³ has described something very similar in the ovarian ova of the Mole, as also have Lindgren⁴, von Sehlen⁵, and Virchow⁶. The part which the enlarged follicular cells of Elasmobranchs play in the nutrition of the ovum is not the direct formation of yolk. Balfour has shown that the yolk originates within the protoplasm of the ovum, and is not transferred thither from the follicular cells. The reasons for this statement are:—(1) that the yolk-spherules first of all appear in the deeper portions of the yolk and not in the more superficial layers, as they would naturally do if they were passed into the interior of the ovum; (2) that there is no trace of yolk-particles in the follicular cells themselves.

Iwakawa's observations on the yolk in the egg of *Triton* lead to a similar conclusion. Götte states that in *Bombinator* the yolk-spherules first make their appearance in the peripheral layers of the ovum, but is inclined to think that they are formed within the substance of the ovum, and that they are not extrinsic in origin. Brock (*loc. cit.* p. 560) quotes and confirms Gegenbaur⁷ to the effect that the yolk-spherules in Teleosts originate by the fusion of minute yolk-particles, and that this formation takes place in the peripheral layers of the ovum; only exceptionally was the neighbourhood of the germinal vesicle the seat of yolk-formation. In Mammalia, according to Balfour the yolk is formed in the peripheral layer of the ovum.

Lepidosiren therefore appears to be remarkable in that the yolk is often formed in the follicular cells and transferred thence to the ovum. Seeing that this is the rule in many of the lower Invertebrata, the occurrence of this method of yolk-formation in *Lepidosiren* would appear to be the retention of an ancestral character.

¹ *Loc. cit.*

² Quart. Journ. Micr. Sci. 1878.

³ Quart. Journ. Micr. Sci. Feb. 1886.

⁴ Arch. f. Anat. u. Phys., Anat. Abtheil. 1877.

⁵ Arch. f. Anat. u. Phys., Anat. Abtheil. 1882.

⁶ Arch. f. mikr. Anat. vol. xxiv. (1884).

⁷ "Ueber den Bau und die Entwicklung der Wirbelthiereier mit partieller Dottertheilung," Müller's Arch. 1861, p. 405. Gegenbaur describes (p. 524) a peculiar fatty degeneration of the follicular cells which serves to loosen them from the ovum when the latter is ready for extrusion. Possibly this is to be referred to a trace of yolk-formation comparable to that described in this paper.

V. Postembryonic Origin of Ova.

This section has been added after the rest of the paper was in type; it deals with the results of some further observations which tend to confirm the supposition hinted at above, that the ovary of *Lepidosiren* contains ova of two kinds which have a different mode of development.

It should have been mentioned that the general surface of the ovary is, for the most part, devoid of any germinal epithelium, a condition which is often met with in adult ovaries; in places, however, the germinal epithelium is very conspicuously present and in a condition of active multiplication. These patches of germinal epithelium are only occasional, as has also been noticed by Spengel¹ in the case of the Frog's ovary; I have only succeeded in discovering them after this paper was communicated to the Society. I have been able, however, to insert a figure into Plate XXVIII. (fig. 7), which illustrates the fact that the germinal epithelium has not entirely disappeared in the mature ovary.

In every case that I observed, the germinal epithelium, where it was left, was in a state of very active cell-division; the cells on the surface of the ovary were closely crowded together, and had given rise to a mass of cells three or four deep, surrounding a cavity partly filled by another mass of cells of a somewhat different appearance. The central mass of cells was invariably connected at one side only with the surrounding sphere, as shown in the figure (Plate XXVIII. fig. 7), and, at this point, its cells gradually alter in appearance until they become indistinguishable from those of the surrounding hollow sphere, which is the future follicular epithelium. The investing mass of cells (*f*) is connected by a pedicle with the germinal epithelium (*e*) on the outside of the ovary, and is clearly formed by a proliferation and inward growth of its cells. The arrangement of these, as shown in the figure, gives a strong impression of motion; the cells look as if they had been arrested in the act of rapid proliferation inwards. The cells of the germinal epithelium, both those on the surface of the ovary and those which form the investing mass of the central cells, are small, but with large, deeply-stained nuclei. On the other hand the cells which occupy the interior of the sphere are much larger, and of a somewhat irregular, angular contour, and often containing more than one nucleus. As already stated, these cells pass by gradations into the follicular mass at one side only, but this may be due to shrinkage. On the outside of the central mass of cells, and forming generally a complete peripheral layer round them, is an amorphous mass (*x*) deeply stained by the reagent; here and there nuclei, with or without some surrounding protoplasm, were imbedded in this amorphous mass, which thus has the appearance of being formed by the fusion of the peripheral layer of the central cells. I have no observations to offer as to the origin of the central mass of cells; but their position and attachment to the peripheral layer, more particularly at one point, would seem to suggest that they arise, like

¹ Semper's 'Arbeiten,' Ed. iii.

the peripheral cells, from the germinal epithelium, but that they are first invaginated and subsequently surrounded by the peripheral layer.

In a later stage the formation of yolk has commenced, and the cells of the central mass are in places separated from each other by aggregations of yolk-particles, though for the most part the cells remain closely adherent; these latter, however, contain yolk-particles in their interior, and the follicular cells, which still form two or three layers, are also filled with yolk. The later stages have been already referred to (p. 283).

It is clear, therefore, that in *Lepidosiren* there are two kinds of ova; those which arise in the way just described may possibly be confined to the postembryonic period.

The mass of central cells with the surrounding follicular layers is clearly comparable to the "Ureirnerster," described by Balfour and others, in many Vertebrates, *e.g.* Elasmobranchs. But although there is this general similarity between the ovary of *Lepidosiren* and that of *Scyllium*, there is evidently a very great difference in detail.

In the Elasmobranch-ovary the nest of primitive germinal cells is imbedded in a mass which consists of the general undifferentiated cells of the germinal epithelium; there is no definite follicular layer at this period. The protoplasm of the primitive germinal cells fuse together, and the nuclei multiply; some of the nuclei degenerate, while others undergo further development, and are eventually separated off from the rest, together with a certain amount of protoplasm, to form ova; the degenerating nuclei are absorbed and aid in the nutrition of the ova. When the ovum is formed, some of the undifferentiated germinal cells range themselves round it and form the follicular layer. A nest gives rise to a variable number of ova. The yolk is formed much later.

In *Lepidosiren* the nest is imbedded in a mass of cells which are definitely marked off from the surrounding cells of the ovary, and can be recognized as the future follicular epithelium; the protoplasm of at least some of the primitive germinal cells fuse together, and the nuclei appear also to multiply, if not the cells themselves in many cases; some of the nuclei degenerate (show a paler colour under the influence of borax carmine) and become irregular in shape; the formation of yolk commences extraordinarily early (as compared with the Elasmobranch) in the mass resulting from the fusion of the peripheral cells, in the remaining cells, and in the follicular layers; the nest gives rise to but a single ovum.

It seems to me impossible to deny that the whole structure (Plate XXVIII. fig. 7), which I have compared to the "nest" of the Elasmobranch ovary, eventually becomes a single ovum; the question that must first be answered is, does the ovum in this case represent a single cell or is it produced by the fusion of a number of cells? The only answer to this question that the facts at my disposal enable me to give is that *these ova are formed by a coalescence of a number of cells out of the nest, the remainder serving as pabulum.* This opinion is so far confirmatory of Götte's observations on the deve-